COÖRDINATION AND MOVEMENT OF THE SWIMMING-PLATES OF MNEMIOPSIS LEIDYI, AGASSIZ

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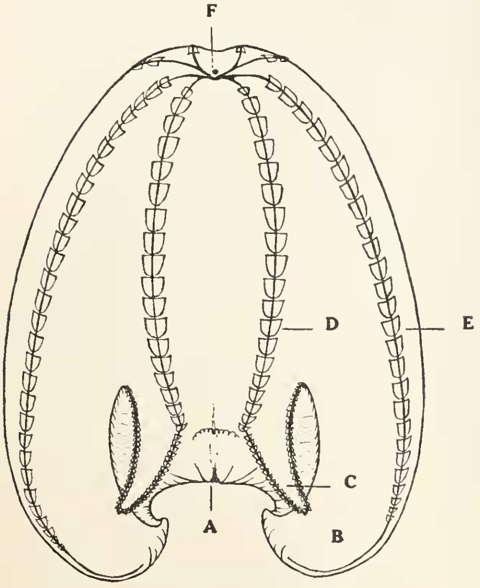
The synchronized movements of the swimming plates of *Mnemiopsis leidyi* in a natural environment indicate the presence of a coördinating system. The rhythm of the plate movement in the rows shows the effect of a coördinating mechanism rather than demonstrating how each plate is stimulated. A single isolated plate containing only a very small amount of protoplasm at its base will beat rhythmically for several hours. This shows that each plate possesses a certain amount of independence, but this independence is overcome by a coördinating system when the body of *Mnemiopsis* is intact. Although Lillie (1906) reported that isolated plates of *Eucharis* continue to beat for several hours and Verworn (1890) recorded the same for *Cestus,* I am convinced that the full significance of this activity has not been realized. It was the persistent beating of these isolated plates, both complete and fragmented, that led me to believe that the transmitting and coördinating system of *Mnemiopsis* has not been fully understood. These experiments have been done, therefore, to add to our knowledge of the transmitting and coördinating mechanism in *Mnemiopsis.*

Ctenophores are biradially symmetrical animals having distinct oral and aboral ends. *Mnemiopsis* is a member of a group of ctenophores which have characteristically a pair of lobes protruding forward beyond the mouth (Fig. 1). This animal moves along in the water just below the surface with its oral end in advance, propelling itself by the successive movements of paddle plates which beat in an aboral direction. Each paddle plate consists of several very long cilia fused and beating as a unit. The plate nearest the aboral end beats first, followed by each plate in succession toward the oral end of the animal (Fig. 3). According to Parker (1905*a*), this type of movement is known as metachronism. The metachronal wave of *Mnemiopsis* is aboral to oral while its effective plate beating is oral to aboral. The plates are arranged on the body of the animal in two opposite pairs of long rows which are in the esophageal plane and are called adesophageal and in two opposite pairs of short rows which are in the tentacular plane and are called adtentacular. On the basis of coördination of the plate movement the rows fall naturally into quadrants each consisting of an adesophageal row and an adtentacular row. The coördination of the two plate rows of a quadrant is quite definite for *Beroe* (Chun, 1880) and for *Pleurobrachia* (Child, 1933). Although the coördination in each quadrant is definite in *Mnemiopsis,* usually all eight rows are synchronized.

That each row of plates in ctenophores represents a transmission path along which stimuli flow to initiate the plate movements is a common belief. This path has been regarded by a few investigators as representing a nervelike, transmitting element not yet differentiated into true nervous tissue but remaining neuroid in form. Bauer (1910) and Bethe (1895) believed the path to be nervous. By staining *Cydippe* with



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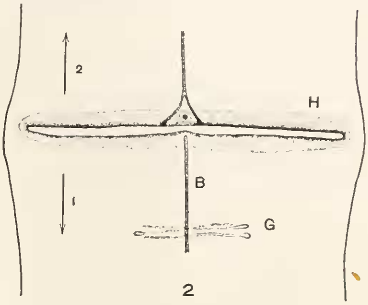

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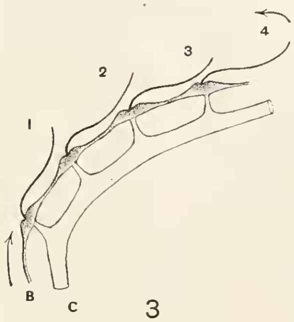

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FIG. 1. A diagram of *Mnemiopsis*. *A*, mouth; *B*, oral lobe; *C*, auricle; *D*, adtentacular swimming plate row; *E*, adesophageal swimming plate row; *F*, apical sense organ in the aboral zone.

FIG. 2. A camera-lucida drawing of a *Mnemiopsis* swimming plate stained with methylene blue; *B*, interplate structure; *G*, muscle cells; *H*, swimming plate base; *1*, arrow pointing in the aboral direction; *2*, arrow pointing orally and in the direction of the metachronal wave.

FIG. 3. A diagram of a swimming plate row showing only a few plates. These plates beat in succession as indicated by the numbers, *1*, *2*, *3*, and *4*. This sequence of movement is known as the metachronal wave. The arrow near *4* indicates the effective stroke direction. The interplate structure is shown at *B*, and the food canal at *C*.

methylene blue and later sectioning the tissue, Bethe found a network of nerves. According to Göthlin (1920), in *Beroe* the activating impulses arise in the nervous system and are conducted by the nerve net to the swimming plate. Ater the impulse reaches the plate it is then transmitted from cell to cell along the plate row. Parker (1905*a*) and Child (1933) believed the initial stimulus in *Pleurobrachia* to come from the sense organ in the aboral zone and spread to the plate rows. The paddle plates of *Mnemiopsis* show definitely a certain amount of coördination. When coming in contact with an object, the body wall contracts, and at the same time the paddle plates cease to beat. The plates resume beating soon afterward and usually by a spreading of their movement from the aboral to the oral zone. This indicates that the center of coördination is in the aboral zone.

In considering the interpretation of the experiments reported here, the following questions arise. Is the aboral sense organ the center of coördination? Does the coördination in each plate row depend entirely upon the stimuli arising in the aboral center? Will this sensory center exhibit its dominance during all rates of plate movements? Is this stimulating element in each plate row strong enough to resist any reversed impulses? Does each plate row exhibit an aboral dominance as reported by Child (1917)? Is the transmitting element nervous or is it less differentiated than nervous tissue? These questions are considered in this report.

Materials and Methods

Mnemiopsis were unusually numerous at Woods Hole from middle August until late September during the summer of 1933. This was due to a wind from the southeast which continued blowing for several days. Uninjured specimens of these ctenophores in stages from late embryos to adults were collected and kept in large finger bowls in running water in the laboratory. Specimens will live in the laboratory for several days only if they are kept in running water. Those of intermediate size were usually selected for observation to determine plate row coördination, while in the experiments in which the plate rows were removed, both large and small animals were used.

The experiments were of three types. In the first type, both large and small pieces of plate rows were stained with methylene blue. In the second type, the action of swimming plate rows was interrupted either by cutting out plates or by holding a plate. In the third type, observations were made on excised pieces of the plate rows.

The Staining Effect of Methylene Blue

The main structures around the sensory body and also those leading from it to the plate rows have been described for *Pleurobrachia, Beroe,* *Bolinopsis,* and *Mnemiopsis* by Child (1933). Only the transmitting elements in the plate rows are to be considered in this section of this report. Parts of the swimming plate rows of *Mnemiopsis* were stained in these experiments. This animal is quite sensitive to methylene blue and will fragment if subjected to other than very dilute solutions. This is in accord with the report of Child (1933). Sections of the swimming plate rows were cut from the animal with small scissors and stained from 2 to 12 hours in a solution of methylene blue of about 1 to 500,000 parts of sea water. These stained pieces of swimming plates were examined in a living condition under both high and low magnifications. The stain showed a structure which connected the plate bases in a row. This interplate structure is a narrow band of granules and is uniform in width except at its enlarged aboral end which contains a small distinct granular spot. The oral end of this band extends into the base of the next plate where it ends clearly without any granular connection to the plate base (Fig. 2). The interplate band lies above and is not connected to the food canal (Fig. 3). Child (1933) has reported the presence of this interplate structure in *Bolinopsis* and in *Mnemiopsis* but he made no mention of the small granular spot.

Although having stained numerous pieces of plate rows of *Mnemiopsis* in methylene blue, I have never found any cellular structure either in these interplate bands or in the plate bases. The only cells brought out by the stain were those of a few muscles lying parallel to and midway between the plates. All other structures shown by the stain were quite granular. The suggestion made by Child that these interplate bands are conducting paths must rest on the position of these bands rather than on their structure. The fact that they point in the direction of transmission may also have influenced Child in making his conclusion. It is clear to me that neither the position of the interplate structures nor their morphological polarity gives sufficient proof of this nerve-like interpretation.

Experiments on the Plate Rows on the Body of Mnemiopsis

The movements of the eight paddle plate rows of ctenophores usually are synchronized. Coördination between two quadrants is more easily destroyed than between the two rows of a single quadrant. Rhythm in a single row is more persistent than it is in a single quadrant. Even this rhythm of the paddle plates in a single row can be temporarily destroyed in *Mnemiopsis* by cutting across any of its plate rows. Very soon, however, rhythm is reëstablished. In one experiment the rhythm in a row was reëstablished within 5 minutes after the cut was made. Usually, when a cut is made, all beating in a row ceases. Then the two rows in a quadrant beat independently for a short time. After this short interval the rhythm in the quadrant is reëstablished. Parker (1905*a*) touched a plate row of *Mnemiopsis* with a pointed instrument. The temporary cessation of beating of the two plates touched was due to the contraction of muscles in the outer body wall closing the plate groove at that point, thus causing a mechanical paddle plate block. When the stimulus was removed, the muscles relaxed and the blocked plates resumed beating. Only the blocked plates failed to beat, while rhythm in the row was not interrupted. Parker held this to be proof that the impulses along the plate row were not aided by the mechanical effect of the paddle plates striking one another as they contract. I verified this experiment by holding a single plate in a row with a stiff hair and found that the rhythm in the row was not interrupted, although the plate which was held did not beat.

The auricles have a row of paddle plates continuous from the adtentacular row to their bases at the oral lobes. These long plates are set very close together (Fig. 1). Each plate touches the one in front when completing its effective stroke and strikes also the one behind in its return stroke. The plates in the adesophageal and the adtentacular rows do not strike one another so effectively. Here was an opportunity to test whether transmission in the row is aided by one plate touching another in beating. Two or three plates were held firmly with a bristle. The action of the other plates was not interrupted in the least. The auricle was then cut across a paddle plate row to a point about midway through the jelly. The cut ends of the plate row were pulled apart by the contracting muscles. Thus a complete gap was formed across the plate row. Beating in the row ceased at first but soon resumed with its usual rate and rhythm. The cutting of either an adesophageal or an adtentacular plate row caused a cessation of plate beating in that row for a brief interval. Almost immediately the rhythm was reëstablished in the plate row followed by that in the quadrant.

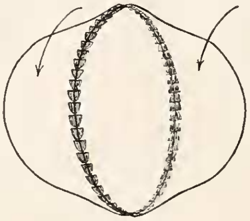
The fact that holding a single plate does not interrupt the rhythm in the plate row shows that transmission does not depend upon movement from plate to plate. This suggests the presence of a real physiological transmitting element. The cutting across any of the plate rows brought about a sudden cessation of plate movement, which suggests that the transmission path is in the plate row. Following the cutting, the rapid recovery of plate movement in the row with the reëstablishment of rhythm indicates that the transmission path is quickly reformed. The question then arises as to whether this transmission path is nervous or is more simple and less differentiated. The rapid recovery of rhythm in the row reveals the more simple nature of this system. The reaction of plates on excised pieces of rows described in the following section also confirms this conclusion.

Experiments on Excised Pieces of Swimming Plate Rows

The beating of the isolated and fragmented plates collected in tow suggests their independence of other paddle plates. This independence was observed in *Eucharis* and reported by Lillie (1906). He stated that quite often the rhythm in the isolated pieces approximated that of the plates in the normal animal. Lillie (1908) cut strips of jelly containing portions of swimming plates from *Eucharis* and from *Mnemiopsis*. According to his observations, soon after the removal, the beating in the excised pieces returned to normal. In my experiments on *Mnemiopsis* the plate activity ceased at once in the strips of plate rows as they were removed. Very soon, however, the beating in these strips was resumed and the waves passed from the aboral end to the oral end. Verworn (1890) reported that a single isolated plate of *Cestus* will continue to beat if it has a small amount of protoplasm attached. It is therefore perfectly clear that swimming plates will beat rhythmically even if they are detached from the ctenophore body. Will isolated plates respond differently to those located normally on the animal?

Sections of both the adesophageal and adtentacular swimming plate rows were cut out of *Mnemiopsis*. Some of the pieces were half of a row in length and others were longer or shorter. Although movement ceased during the cutting, activity was resumed in the pieces within 10 minutes after their excision. Both the effective stroke and the metachronal wave were the same as before the pieces were removed. The rhythm was unchanged and, although the rate was reduced at first, the normal speed was soon regained. Within one hour each piece had formed a complete compact body. In general, three types of bodies were formed by these excised pieces. When a small amount of jelly was removed with approximately one-half of a plate row, the reformed body was egg-shaped. The plate row was oriented midway around the mass on its shortest axis (Fig. 4). Practically the same results were obtained when a larger amount of jelly was removed with half a plate row, though the jelly in this case did not completely fuse at its cut ends (Fig. 5). In both these cases, the ends of the paddle plate rows always fused perfectly. When a still larger amount of jelly was removed with one-half a plate row, the reformed body was more elongated and the cut ends of the jelly were less completely fused than in the previously described cases. This incompletely fused jelly left a cavity large enough to prevent the fusing of the ends of the plate row (Fig. 6). All pieces of jelly containing paddle plates lived and continued their beating for two weeks. They were then thrown away, though still in good condition.

The effective beating of the paddle plates in all of these cases caused the individual pieces to rotate. Mechanically, the rotation must be directly opposite to the direction of effective beating of the swimming plates. Hence, by observing the direction of movement of the rotating pieces, the direction of the effective paddle plate beating can be determined. If a revolving excised piece of swimming plate is touched anywhere with a needle, the whirling stops at once, but the plate beating is resumed in a short time. Often this resumed paddle plate action causes the whole piece to rotate in the opposite direction, giving definitely a demonstration of reversed ciliary beating in *Mnemiopsis*. This reversal may continue until a dozen revolutions have been made. Then, without being stimulated further, all movement ceases for an instant and the regular beating follows. This reaction is common in all three types of reformed plate rows. I have never seen a metachronal wave reversal



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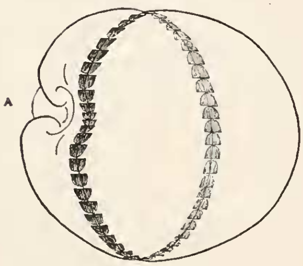

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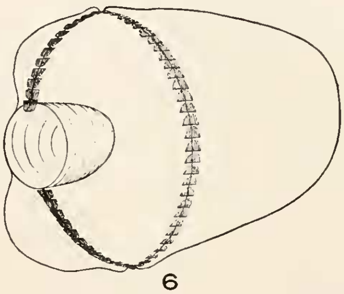

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FIG. 4. This shows the rounded jelly and the swimming plate row after its cut ends have completely fused to each other. The arrows indicate the direction in which the piece rotates.

FIG. 5. At *A* the incomplete fusion of the jelly is shown. The swimming plate row ends have fused to each other completely.

FIG. 6. This illustrates the incomplete fusion of the jelly and of the cut ends of the swimming plate row. The direction of rotation in both Figs. 5 and 6 is the same as in Fig. 4.

in any of the pieces. Moreover, a reversal of metachronism in a normal plate row of *Mnemiopsis* has never been reported. Parker (1905*a*) noticed an apparent reflection of the wave as it reached the oral end of a plate row in *Pleurobrachia*. This reflection wave rarely traveled aborally the entire length of the plate row.

Both large and small individuals were cut transversely midway between their aboral and oral ends. Immediately following the cutting the paddle plates in both halves stopped beating. The plate action was resumed in the aboral halves within 10 minutes and the rhythm was reestablished at once. Beating was not resumed in the oral halves until a few minutes later, and then action of the paddle plates in these halves was not synchronized as in the aboral pieces. The plates beat slowly at first and quite independently of one another. Within 24 hours the normal rhythm had been established in these oral halves, however. In one oral half, a complete aboral end had been reformed within 48 hours. This reformed zone was perfect, including the sense organ and food canal connections from the stomach to the paddle plate rows. More experiments of this nature have been planned.

The definite polarity in the intact plate rows of *Mnemiopsis* indicates a higher type of transmitting system, but when the polarity is destroyed in excised pieces of these plate rows, the more elementary nature of this system is revealed. Furthermore, the ability of the jelly and the transmission system to reform quickly following a cut indicates that both of these structures are not very highly differentiated. Therefore, these experiments on excised pieces of plate rows of *Mnemiopsis* show that its transmitting system is simple and elementary in nature.

Discussion

According to those who have studied stained sections and stained regions of ctenophores, it is clear that the coördinating mechanism is nervous. Bethe (1895) showed a network of nerves to be present in the epithelium of *Cydippe*. Chun (1880) failed to find true nervous tissue in the ciliated furrows leading from the sensory region to the plate rows; but he believed this tissue to be nerve-like in transmitting impulses. Child (1933) found a clear picture of the nervous structure about the apical organ of *Pleurobrachia*, *Beroe*, *Bolinopsis*, and *Mnemiopsis* by staining them with a weak solution of methylene blue in sea water. He states (page 204), "There can be little doubt that these structures represent a real, morphologically differentiated nervous system." He failed, however, to find a definite structure, by staining, between the plates of *Pleurobrachia*. The stain showed granules in the outer body wall between the plates. The irregular arrangement of these granules could not indicate a definite transmitting structure. Child found definite structures between the plates of *Bolinopsis* and *Mnemiopsis* which he interpreted as nerve terminations. I have found these staining bodies in *Mnemiopsis,* but, although they are definite as granules (Fig. 2), I question any justification in assuming them to be nervous from their staining qualities alone, since methylene blue usually shows true nervous tissue to be cellular. This structure is in the epithelium above and independent of the food canals and is quite definite (Fig. 3). The granules were just as clear around the bases of the swimming plates as they were between these plates. Do these granular bodies around the plate bases represent nerves also? If so, these nerves are of a peculiar type since there are no indications of cells. I see no reason for calling either the interplate structures or the granular mass around the plate bases true nervous tissue, but some type of transmitting element is certainly present along the swimming plate rows as has been shown by physiological tests.

That the regulating center lies in the aboral zone is well established. In *Mnemiopsis,* usually the eight paddle plate rows are synchronized. At times when the animal is not moving and the rate of beating is decreased, a row of plates will beat independently of the others. Then we must assume that the regulating center in the aboral zone loses control with the lowering of the rate of beating. The coördinating mechanism in a single row is more definite physiologically than is the aboral center. In each row, the plates are synchronized perfectly even at the low speeds of movement. Even if a plate or two in a row be either cut out, held firmly, or cooled, the rhythm in a single row of *Pleurobrachia* is not interrupted (Parker, 1905*a*). According to Parker, the individual plate rows of *Pleurobrachia* are often independent of the others. The beating of the plates on the auricles is usually not synchronized with the beating of the other plate rows, nor do they beat at the same rate. Furthermore, the metachronal wave in the auricle is rarely continuous. Usually, this wave begins at the auricle tip, moving on one side to the adtentacular plate and on the other side to the oral lobe. These facts show further the localized nature of the transmitting and coördinating elements in *Mnemiopsis.*

The transmitting system, as indicated by the metachronal wave, in *Mnemiopsis* is polarized. Impulses proceed along the plate rows from the aboral zone to the oral zone. In the uninjured animal living in its natural environment, this transmission direction is never reversed. Reversal of the metachronal wave in *Pleurobrachia* occurs occasionally, but this could not be induced in *Mnemiopsis* (Parker, 1905*a*). Reversal of the effective beat does not occur in *Mnemiopsis* (Parker, 1905*a*:

Mayor, 1912), and it occurs only rarely in *Bolinopsis* (Child, 1933). Reversal of the effective beating of cilia of sea anemones is commonly known (Parker, 1905*b*, 1905*c*, 1917; Parker and Marks, 1928). Since ctenophores are related to the actinians, this led me to seek the evidence of paddle plate reversal in *Mnemiopsis.*

The excised pieces of *Mnemiopsis* previously described in this paper (Figs. 4, 5, and 6) certainly show a reversal of the effective paddle plate beat. It is mechanically impossible for the piece to reverse its direction of whirling without reversing also the effective paddle plate beating. The pieces used in this experiment remained on the one side while rotating. This reversed whirling followed any type of touching stimulus. Furthermore, the stimulus had the same effect whether it was applied anywhere on the jelly or directly on the paddle plate row. As far as could be observed, the aboral plate was the first to beat at the beginning of the normal metachronal wave and also at the beginning of the reversed effective beat. This gives proof to the dominance of the aboral region, which is in agreement with Child (1917). I did not see reversal of the metachronal wave of the paddle plates in the excised pieces of *Mnemiopsis.* Reversal of the metachronal wave in *Pleurobrachia* has been observed by Child (1933), who associated the lower degree of reversibility in the lobate forms with their higher degree of differentiation of the transmitting path.

When *Mnemiopsis* was cut transversely, dividing the animal into oral and aboral halves, the plates in the aboral half regained their rhythmic beating first. The fact that rhythm is slowly reëstablished in an oral half shows further the dominance of the aboral zone. Though the oral half established rhythmic beating within 24 hours, this was undoubtedly due to the reorganization of the tissue to reform the aboral center, since this center was completely reformed within 48 hours. Because of this rapid reformation of transmitting tissue, cutting a single plate from a row does not interrupt the rhythmic beating. This reorganization must have occurred in *Beroe* during the experiments of Eimer (1880), who observed the movements of the oral half to be indistinguishable from those of the aboral half. Lillie (1914), who cut strips of paddle plates from *Eucharis,* reported that they rounded up in much the same manner as did pieces of *Mnemiopsis* in my experiments. He stated that the two ends of the paddle plate row failed to fuse. This was true in pieces of plate rows of *Mnemiopsis* (Fig. 6). Lillie saw that the beating wave continued even over the open space in the jelly and concluded the impulse to be an electrical one which might well be transmitted across the gap through the water. A rapid reformation of the tissue in cut regions of *Mnemiopsis* demonstrates the possibility of the reformation of the transmitting structure around the gap. This, then, instead of electrical impulses passing through the water, accounts for the transmission of impulses across the gap in pieces of *Eucharis*.

SUMMARY

1. The apical organ in the aboral zone is the center from which impulses travel out into the plate rows.

2. The aboral impulses synchronize the plate movements in all eight rows except during slow movements.

3. At low rates of plate beating each row becomes independent.

4. The synchronism in the plate rows of a quadrant as a unit is more persistent than in the eight plate rows as a unit.

5. The highest type of synchronized unit is demonstrated by a single plate row.

6. A single plate row beating independently of other plate rows, whether normally located on the animal or detached from it, exhibits an aboral dominance.

7. Swimming plates do not reverse either their metachronal or effective beat while located naturally on the animal.

8. Swimming plates reverse their effective beat on isolated pieces of plate rows, but they do not reverse their metachronal wave.

9. Dilute solutions of methylene blue show the interplate structures in the plate rows to be entirely granular in nature without exhibiting any cellular elements.

10. The coördinating system of *Mnemiopsis* is demonstrated more definitely by physiological tests than by staining results. This system is superficially located along the plate rows. The fact that single isolated plates show a certain amount of autonomy and the fact that transmission in a plate row is immediately reëstablished following its interruption as produced by a cut show this system to be much more localized than has been heretofore believed.

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